

# The Sexual Cycle and Reproductive Modality in *Littorina saxatilis* Olivi

(Mollusca : Gastropoda)

BY

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(4 Text figures)

## INTRODUCTION

*Littorina saxatilis* Olivi, 1792 is a highly polymorphic species within which many subspecies and varieties have been described (DAUTZENBERG & FISCHER, 1912; JAMES, 1968). One subspecies, *Littorina nigrolineata*, has such well defined ecological, morphological, and physiological characteristics that it has been held to be a distinct species (SACCHI, 1975; HELLER, 1975). The chief diagnostic characteristics for species distinction have been within the reproductive modality, as demonstrated by DEYGLUN (1955): *L. nigrolineata* is oviparous, while *L. saxatilis* is generally considered to be ovoviviparous. The most definitive confirmation of specific status has been electrophoretic analysis of the leucine aminopeptidase (CAUGANT & BERGERARD, 1979).

The sexual cycle of Littorinidae has been especially well investigated in *Littorina littorea*. LINKE (1933) described a sexual rest-phase in males, with an absence of the penis. Unlike other species of marine gastropods, in *L. littorea* the penis is not resorbed but is shed at the end of the breeding season (GRAHAME, 1969). STREIFF & LE BRETON (1970) have demonstrated an endocrinological control of both penis regression and penis morphogenesis.

While BERRY (1961) has described an analogous cycle in *Littorina saxatilis*, with regression of the genital organs of male and female in the summer, BERGERARD (1971) has shown that the cycle varies in different populations. Study of a population in Brittany (north of the "Île de Batz") showed that regression occurs only in old animals (BERGERARD, 1975).

Concomitant with an electrophoretic analysis of isozymes, the sexual state of several populations of *Littorina saxatilis* on the north coast of Brittany has been determined at different times of the year; samples of 100 individuals from each locality were examined. The populations included those of the variety *rudis* from rocky shores with various degrees of exposure to wave action and a population from a sandy shore habitat, where only the "typical" form, identical to those of the lagoon of Venice, was found.

## SEXUAL CYCLE IN MALES

Three sexual stages were defined in the males, on the basis of degree of development of the penis, testicle, and seminal vesicle: immaturity, maturity, and regression. The per cent of maturity in a population (the proportion of reproductively capable males) was computed as follows:

$$\frac{(\text{Number of mature males})}{(\text{Total number of males}) - (\text{Number of immature males})} \times 100$$

The variations of per cent maturity throughout the year for 3 populations on rocky shores (Bloscon, Brignogan, and Pors-Hir) and for the population on a movable substrate (Bight of Kernic) are shown in Figure 1.

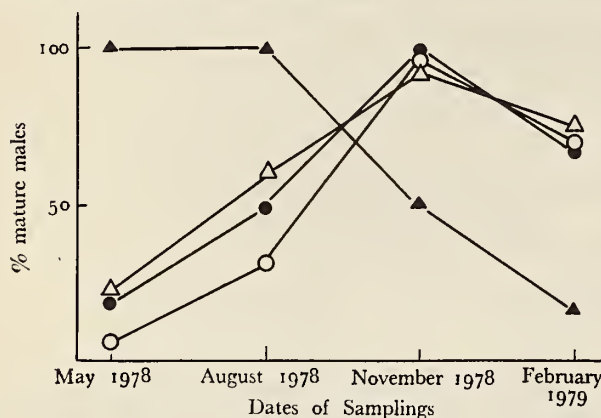


Figure 1

Variations in the per cent of maturity in males throughout the year Stations:

Bight of Kernic ▲ Pors-hir △  
Brignogan ● Bloscon ○

For the *rudis* variety, the sexual cycle is similar at the 3 stations, with a maximum maturity (close to 100%) in November, and a maximum regression in May. The population at Bloscon, which was followed for 2 years, showed a similar cycle each year. On the other hand, the population of typical *Littorina saxatilis* at the Bight of Kernic locality displayed a maximum maturity in summer (May and August), then regressed from November onward, reaching a minimum of mature males in February. Thus, the cycle in this population appears to be the reverse of that in *L. saxatilis rudis*.

## SEXUAL CYCLE IN FEMALES

Four sexual stages were defined in the females, on the basis of ovary, annex gland, and brood pouch development: immaturity, gestation (i.e., incubation), maturity without gestation, and regression. The per cent of maturity in a population was determined as follows:

$$\frac{(\text{Number of incubating females}) + (\text{Number of mature but non-incubating females})}{(\text{Total number of females}) - (\text{Number of immature females})} \times 100$$

The per cent of gestation was computed by:

$$\frac{(\text{Number of incubating females})}{(\text{Total number of females}) - (\text{Number of immature females})} \times 100$$

Figures 2 and 3 show variation in these parameters during the year. The cycle of females (Figure 2) appears to be more complex than that of males: two populations show fairly similar cycles (Bloscon and Brignogan), with a minimum of maturity in August and 100% maturity in February, coinciding with the cycle of the males in the same population. However, the other population of the *rudis* variety, from Pors-Hir, reached maximum maturity in August, while the values for the 3 other samples are relatively the same as those for the previously mentioned stations. There is also a similarity in the per cent of gestation in the Bloscon and Brignogan populations (Figure 3): they were low during the whole year (always below 50%) and showed no cyclic variation. This may have led to the belief that the females, in some populations, do not have a sexual cycle (PELSENEER, 1934). At Pors-Hir, the August sample showed an increased per cent of incubating females (nearly 90%); this would explain the peak of female maturity at this period. As was noted for the per cent of maturity, the 3 other samples were similar to those at Bloscon and Brignogan. The three populations of *Littorina saxatilis rudis* showed a minimum of mature but not incubating females in August.

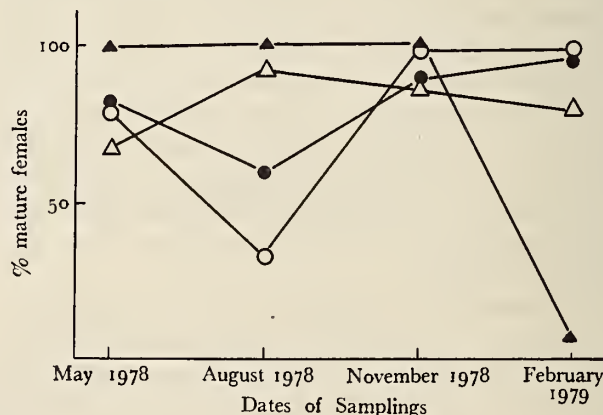


Figure 2

Variations in the per cent of maturity in females throughout the year Stations:

Bight of Kernic ▲ Pors-hir △  
Brignogan ● Bloscon ○

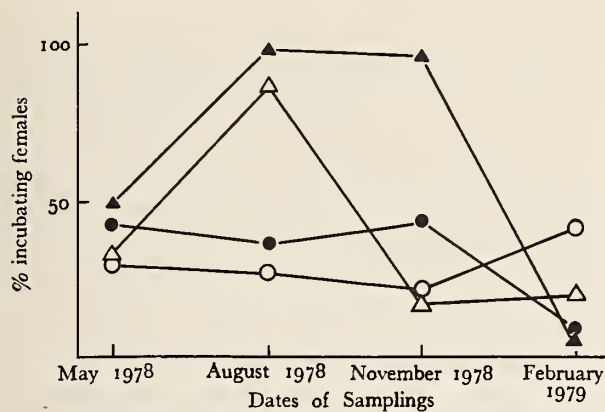


Figure 3

Variations in the per cent of gestation throughout the year

Stations:

Bight of Kernic  
Brignogan

▲  
●

Pors-hir  
Blosscon

△  
○

The female population at the Bight of Kernic also behaved very differently from the other populations. All individuals were mature in May, August, and November, and the population exhibited a great regression in February. It is important to note here that when females show regression of the ovary and annex glands, the majority is still in gestation; the brood pouch often contains some well developed embryos. In this case, the regression mechanism appears to be somewhat different, as it begins even before the brood pouch is completely empty.

The proportion of incubating females to mature females ranged from 40% to 50% for the *rudis* variety and was more than 80% for typical *Littorina saxatilis*.

(adjacent column →)

Figure 4

Breakdown of the population of Pors-Hir by shell height for the various sexual states in August and November, 1978

Sexual states:

immature female



incubating female



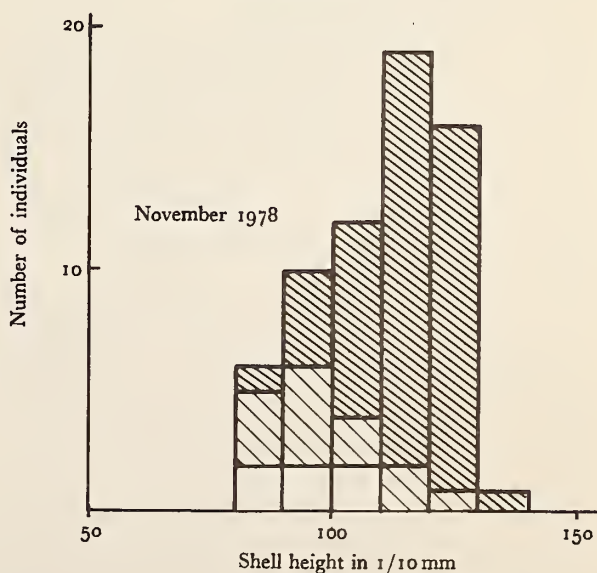
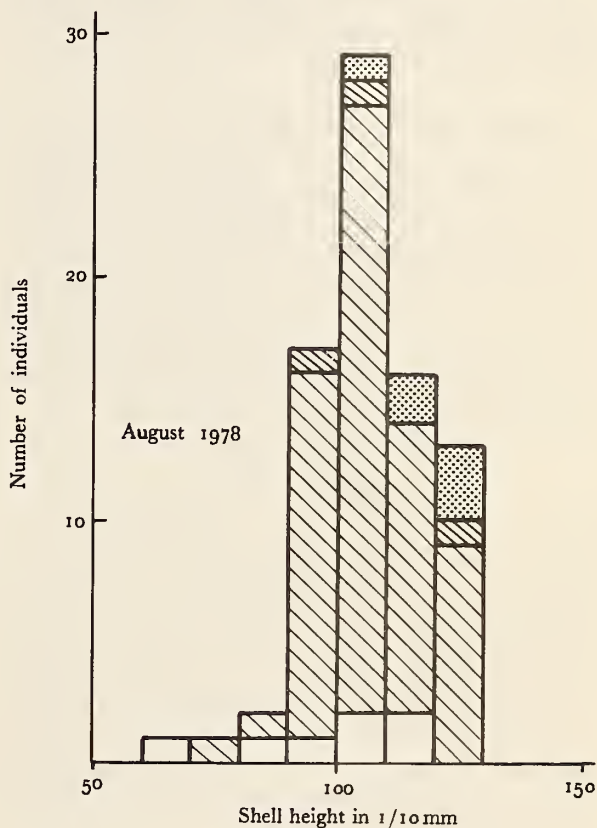
mature female without embryos,  
similar to oviparous female



regressed female



Figure 4 shows a breakdown of the female population at Pors-Hir by size for the various sexual states during August and November, 1978. While in August most of the





females with shell height greater than 9 mm were incubating, in November those greater than 10 mm were mature, but non-incubating. While the young females are still incubating, most have reached a state of maturity quite analogous to females of the oviparous species *Littorina nigrolineata*.

Animals derived from various Breton populations of *Littorina saxatilis* (Île Grande, Bloiscon, Île Callot) were raised individually so that the spawning process could be observed in each. In these populations, animals which had shells similar to those of the ovoviviparous *L. saxatilis* produced spawns like *L. nigrolineata* and with a high frequency. As in *L. nigrolineata*, young animals emerge directly from spawns without passing through a pelagic stage. The time required for embryonic development also seems similar (about one month).

## DISCUSSION

Oviparity in *Littorina saxatilis* was first observed by SESHAPPA (1947) in the form *rudissima*. In 1948, he concluded that, "here is a case of the same species exhibiting both the oviparous and the viviparous modes of reproduction even in the same locality," a phenomenon previously observed in several species of Gastropoda: *Helix carthusiana*, *Achatina panthera*, *Balea perversa* (PELSENEER, 1935, cited by SESHAPPA, 1948). This conclusion subsequently was contested on the grounds of mistaken identity, i.e., confusion with *L. nigrolineata*.

In 1978, HANNAFORD-ELLIS described a new species, *Littorina arcana*, morphologically identical to *L. saxatilis* and sympatric with it, but differing in mode of reproduction. She noted a ciliated field which differs in extent in the viviparous and oviparous females (1979). Since this "field" is situated close to the jelly-gland, which changes into the brood pouch in ovoviviparous females, its value as a specific character seems contestable, especially since in males it is involved with prostate development.

Two modes of reproduction in the same species seem much more likely: indeed, electrophoretic analysis of the incubating and mature but non-incubating females reveals no significant difference for 3 enzymatic systems: esterases, leucine aminopeptidase, and glucose-6-phosphate dehydrogenase; these are the enzymatic systems which allowed differentiation of *Littorina nigrolineata* (CAUGANT, 1979).

In addition, as shown by the changes in the sexual stages of females in Pors-Hir between August and November, 1978 (cf. Figure 4), it must be admitted that some animals do indeed pass from viviparity to oviparity since most of

the females passed from one stage of maturity to the other. This does not require significant modification of the female genital system, since only the jelly gland is modified in the ovoviviparous form (GAILLARD, 1977; WEBBER, 1977).

The capacity to adopt other reproductive patterns during certain periods of the year has selective advantage for the species. Indeed, if oviparity increases the reproductive capacity of the individual (HUGHES, 1978), ovoviviparity during the summer would provide the best protection against desiccation.

The reproductive modality of *Littorina saxatilis*, therefore, appears not to be as fixed as has been believed. Oviparity exists in most of the populations. Nevertheless, an exception has to be made for the population of the Bight of Kernic, in which the per cent of gestation is very high throughout the year. This population is also exceptional with regard to the *rudis* variety, because there is an average 6-month delay in the sexual cycle for males as well as for females; the regression of the genital system occurs in winter.

In the 3 populations of *rudis*, the male sexual cycle does not vary: exposure of the stations to wave action does not influence the cycle. On the other hand, the female cycle shows much greater variations among stations. This confirms BERGERARD's observations (1971). This variation could result from higher mortality in exposed localities, so that the cycle is frequently incomplete.

If the mean sizes of the incubating females and the mature but non-incubating females in Pors-Hir are compared, there is a significant difference ( $P = 0.01$ ), since incubating females are on the average smaller than non-incubating females (10.6 against 11.4 mm). This difference is equivalent to the increase in mean size of the animals in a few months (DAGUZAN, 1975; MORETEAU, 1976). So it is difficult to decide whether the passage from one mode of reproduction to another is reversible. This conversion appears to be influenced both by the age of the animal and by the ecological conditions at the stations.

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